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The Structure of the Planktonic Food-Web in the St. Lawrence Great Lakes

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ABSTRACT. *The structure of the planktonic food-web was studied during the spring (April/May) and summer (August) periods in 1993 to 1995 at twelve stations located in the offshore region of all five Great Lakes. All components of the planktonic food-web were collected from the same water sample (with the exception of crustaceans), counted microscopically, converted to carbon units, and averaged over the euphotic zone. Due to phosphorus load reductions and the impact of non-indigenous mussels in the lower lakes, physical/chemical characteristics of the lower lakes are becoming similar to those in the upper lakes. Spring total phosphorus and euphotic zone depth were relatively similar among all the stations (except western Lake Erie), ranging from 3 to 7 μg/L and 21 to 26 m, respectively. During the summer, total phosphorus concentrations were more variable, but ranged between 4 to10 μg/L at all stations except western Lake Erie. Planktonic biomass was correlated with total phosphorus concentration. Within a season, the structure of the planktonic food-web was remarkably similar among all stations across all the lakes. Of the seventeen food-web structure parameters examined, only two exhibited significant differences among stations during the spring isothermal period; only four parameters exhibited significant differences among stations during the summer. Small plankton were very abundant in all the lakes. Picoplankton (0.2 to 2.0 μm) biomass was approximately equal to the combined biomass of nanno- and microplankton (2 to 200 μm). For microorganisms (all organisms except crustaceans) autotrophic: heterotrophic ratios averaged 1.3 (spring = 1.1, summer = 1.5). The heterotrophic microorganism community was comprised of bacteria (mean = 65%), protozoans (mean = 32%), and rotifers (3%). Even though zebra mussel veligers were found in all the lakes except Lake Superior, their contribution to microorganism biomass never exceeded 1%. Due to seasonal variation in crustacean abundance, the mean contribution of major functional groups varied by season; producers (autotrophs), decomposers (bacteria), micrograzers (protozoans and rotifers), and mesograzers (crustaceans) constituted 40%, 30%, 11%, and 19% of total planktonic carbon, respectively, during the spring, and 32%, 15%, 9%, and 43%,*

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respectively, during the summer. The overall similarity in the structure of the planktonic food-web across all stations in the Great Lakes was attributed to the strong influence of abiotic factors.

***INDEX WORDS**: Microorganisms, planktonic food-web, Great Lakes, autotrophic, heterotrophic, picoplankton.*

INTRODUCTION

The unique nature of the St. Lawrence Great Lakes has contributed to a long and productive history of research. The early history of this research was described in much detail by Beeton and Chandler (1963) and Beeton and Schneider (1998). Most of the early planktonic work, prior to the 1960s, was primarily descriptive in nature (Davis 1966). The late 1960s and 1970s were a golden era of Great Lakes research, when concern for eutrophication and the collapse of several fisheries served as the impetus for several large interdisciplinary research programs, the most notable being the study of Lake Ontario during IFYGL (International Field Year on the Great Lakes) (Ludwigson 1974). Because much of the concern was centered on nutrient overenrichment, many plankton studies were initiated during this period (e.g., Watson and Carpenter 1974, Munawar and Munawar 1975, Stoermer and Ladewski 1978). Our understanding of plankton ecology increased substantially during this period resulting in several published reviews of the plankton communities in the Great Lakes (Vollenweider *et al.* 1974, Watson 1974, Munawar and Munawar 1982).

The 1980s were a period of significant new insights into the structure of the planktonic food-web as well as of significant new perturbations. Prior to this decade, the planktonic food-web in the Great Lakes was typically described with traditional phytoplankton and zooplankton groups (Scavia 1980). The discovery of an abundant and important microbial food-web in the 1980s forced a reevaluation of existing concepts of food-web structure and function in the Great Lakes (Lean *et al.* 1987, Scavia and Fahnenstiel 1988) and all aquatic environments (Azam *et al.* 1983, Fenchel 1988, Hairston and Hairston 1993). With the development and application of new techniques, particularly fluorochrome staining combined with epifluorescence microscopy (Hobbie *et al.* 1977, Haas 1982, Caron 1983), researchers discovered abundant populations of autotrophic and heterotrophic picoplankton (organisms < 2 μm) and protozoans in the Great Lakes (Caron *et al.* 1985, Fahnenstiel *et al.* 1986, Scavia *et al.* 1986, Pick and Caron 1987, Carrick and Fahnenstiel 1989). Also in the 1980s, several non-indigenous species that had the ability to significantly alter the planktonic community were introduced into the Great Lakes. Although the Great Lakes have had a long history of invasion by non-indigenous species (Mills *et al.* 1993), most of those having had substantial impact on the Great Lakes had been fish, e.g., lamprey, alewife, etc. (Mills *et al.* 1993); however in late 1980s and early 1990s several important non-indigenous invertebrates arrived in the Great Lakes, including the zebra mussel (*Dreissena polymorpha*), quagga mussel (*Dreissena bugensis*), and spiny water flea (*Bythotrephes cederstroemi*). Major changes in the abundance and composition of the plankton food-web in the Great Lakes have been attributed to these invertebrates (Leach 1993, Dermott and Munawar 1993, Lehman and Caceres 1993, Mills *et al.* 1993, Makarewicz *et al.* 1995, Nalepa and Fahnenstiel 1995).

Because of the profound impact of these new, non-indigenous species and the widespread availability of new techniques to enumerate all components of the planktonic food-web, a comparative study of the Great Lakes was conducted from 1993 to 1995. Using consistent techniques and in most cases the same water sample, the community structure of the entire planktonic food-web (organisms in size from 0.2 μm to 2.5 mm) of all five of the Great Lakes was examined. Even though this work focused on broad-scale patterns based on taxonomic, size and functional analyses, all organisms were counted individually using appropriate microscopy. This paper marks the first attempt to characterize the entire planktonic food-web in all five Great Lakes and document the broad-scale structural food-web similarities that exist among all five of the Great Lakes.

METHODS

Sampling was conducted at 12 stations in the St. Lawrence Great Lakes aboard the R/V Laurentian (Fig. 1, Table 1). Two to three stations in the offshore region of each lake were sampled. With the exception of the Lake Superior stations, all stations were sampled during two cruises (April/May and

FIG. 1. Location of sampling stations.

August periods) of each year, 1993 to 1995. Thus, each station was sampled six times during this study. Lake Superior stations were sampled only during the August 1994 cruise.

At each station, a Seabird CTD cast with fluorometer and transmissometer (25-cm beam path) with a 2-Hz sampling rate was made from the surface to just above the bottom. The CTD profiles were used to determine the discrete sampling depths for plankton collections whenever the water column was stratified. Secchi disk transparency was measured with a black/white 25-cm disk. Underwa-

TABLE 1. Physical/chemical characteristics of the sampling stations. Mean euphotic zone depth and total phosphorus values are presented along with standard errors. Euphotic zone depth was calculated from PAR extinction coefficients or converted beam transmittance values.

Station Name	Station Number	Station Depth (m)	Spring Euphotic Depth (m)	Summer Euphotic Depth (m)	Maximum Euphotic Depth (m)	Spring Total Phosphorus (µg/L)	Summer Total Phosphorus (µg/L)
L. Erie-West	E1	7 m	13 ± 0.5	13 ± 0.9	14	14 ± 3.0	19 ± 4.8
L. Erie-East	E2	57 m	23 ± 1.2	18 ± 1.7	26	5.7 ± 1.0	6.5 ± 0.6
L. Ontario-West	O3	133 m	25 ± 0.8	16 ± 1.1	26	6.2 ± 1.2	10 ± 1.2
L. Ontario-East	O4	159 m	26 ± 1.5	14 ± 1.6	29	6.6 ± 1.4	8.6 ± 0.7
L. Michigan-South	M5	107 m	21 ± 1.4	26 ± 2.6	31	6.0 ± 1.4	5.4 ± 0.2
L. Michigan-North	M6	144 m	24 ± 0.7	26 ± 0.8	28	4.9 ± 1.2	7.3 ± 1.2
L. Huron- South	H7	37 m	25 ± 1.5	29 ± 2.2	33	3.9 ± 0.7	5.4 ± 0.8
L. Huron- Central	H8	68 m	27 ± 0.5	28 ± 1.5	31	3.5 ± 0.6	4.6 ± 0.7
L. Huron- North	H9	64 m	26 ± 0.5	29 ± 1.0	31	3.2 ± 0.3	5.1 ± 0.7
L. Superior-East	S10	201 m		42	42		5.6
L. Superior-Central 1	S11	220 m		42	42		4
L. Superior-Central 2	S12	218 m		46	46		

ter light extinction of photosynthetic active irradiation (kPAR) was measured with a LICOR 193SB scalar (4≠) light sensor and LICOR-1000 data logger and/or a Biospherical integrating natural fluorometer equipped with a downwelling scalar PAR sensor. At stations that were sampled during darkness, beam attenuation values were converted to extinction coefficients using the conversion of Fahnenstiel *et al.* (1995) developed in Saginaw Bay with the same transmissometer. These kPAR values were used to calculate the depth of the euphotic zone (1% isolume) .

In order to minimize extraneous light effects on phytoplankton communities, plankton sampling was conducted in almost all cases at night, usually 1 to 4 hours before dawn. From the CTD profiles, vertically distinct layers were selected for sampling, e.g., epilimnion, metalimnion, and deep chlorophyll layer. At each station (with exception of western Lake Erie) discrete samples were taken from 3 to 6 depths in the euphotic zone using a Niskin bottle and poured into a 24-L carboy (one carboy for each depth). All water samples were taken from these carboys. Because of the shallow water in western Lake Erie (7 m), samples were collected from only two discrete depths. Chlorophyll samples were filtered onto Whatman GF/F filters, extracted with N, N-dimethylformamide, and analyzed fluorometrically (Speziale *et al.* 1984). Total phosphorus samples were digested with potassium persulfate and analyzed by the molybdate/ascorbic acid method (Davis and Simmons 1979).

The methods for preserving, preparing, and counting microbial communities have been described in detail (Scavia *et al.* 1986, Fahnenstiel and Scavia 1987, Carrick and Fahnenstiel 1989, Carrick and Fahnenstiel 1990, Fahnenstiel and Carrick 1992) and will only be briefly described here. Plankton samples from discrete water collections were preserved in amber bottles as follows (all concentrations are final concentrations): Heterotrophic and autotrophic picoplankton, 2% glutaraldehyde; phytoplankton, 0.5% Lugol's solution; flagellated protozoans, glutaraldehyde (2%) buffered with sodium cacodylate (0.1 M); ciliated protozoans, 1 to 2% Lugol's solution; rotifers and veligers, narcotization with club soda and preservation with 5% buffered formalin. All aldehyde-preserved samples were immediately stored at 5°C until preparation of microscopic slides. Duplicate permanent or semipermanent slides were prepared (picoplankton, protozoans, and phytoplankton). All slide preparations for epifluorescence microscopy (heterotrophic bacteria, autotrophic picoplankton, and protozoans) were made within 24 h of collection, stored in a freezer until the end of the cruise, and then counted as soon as possible.

Heterotrophic bacteria were enumerated with the AODC method (Hobbie *et al.* 1977). Preserved samples were stained with acridine orange, filtered onto Irgalan black-stained 0.22-μm polycarbonate filters, and mounted onto slides with immersion oil. A minimum of 300 cells were counted with a Leitz Laborlux 12 microscope or Aus Jena Research microscope equipped for blue excitation (450 to 490 nm; beam splitter 510 nm). At least 30 bacteria cells from each sample were measured from projections of photomicrographs. Volumes were determined and converted to carbon using the conversion factor of 0.38 pg/μm^3 (Lee and Fuhrman 1987).

Autotrophic picoplankton samples were enumerated with epifluorescence microscopy to distinguish the dominant autofluorescent emission of each cell (Fahnenstiel and Carrick 1992). Preserved samples were filtered onto 0.2-μm Nuclepore filters and mounted onto slides with immersion oil. An Aus Jena Research microscope equipped with blue (450 nm) and green excitation (530 to 560 nm) was used to enumerate prokaryotic and eukaryotic autotrophic picoplankton. At least 300 cells were counted on each slide and at least 30 cells were measured from projections of photomicrographs. From these measurements, cellular volumes were calculated and converted to carbon units using the conversion factor of 0.38 pg/μm^3 for cyanobacteria (Lee and Fuhrman 1987) and 0.36 pg/μm^3 for eukaryotic picoplankton (Verity *et al.* 1992).

Flagellated protozoans were enumerated with the primulin technique (Caron 1983, Carrick and Fahnenstiel 1989). Preserved samples were filtered onto 0.8-μm black membrane filters, rinsed with Trizma buffer, stained with primulin, and mounted onto slides with immersion oil. A minimum of 300 organisms were counted using a Leitz Laborlux or Aus Jena microscope equipped for both UV (320 to 380 nm) and blue excitation (450 to 590 nm). Ciliated protozoans were enumerated with the Utermohl technique (Ütermohl 1958, Carrick and Fahnenstiel 1990). Preserved aliquots (25 to 50 mL) were settled onto coverslips, and the entire area of the slide was scanned at 200X with an inverted microscope. Cell volumes for protozoans were estimated by determining average cell dimensions from a minimum of ten randomly chosen individuals of each taxa and applying these dimensions to the

most appropriate shape (e.g., prolate spheres, cylinders). Protozoan carbon values were estimated from biovolumes using the equation ($C = 0.433 (BV)^{0.863}$) from Verity *et al.* (1992).

Phytoplankton samples were filtered onto microscope slides according to the procedure of Dozier and Richerson (1975) used previously for Great Lakes phytoplankton (Fahnenstiel and Scavia 1987, Fahnenstiel and Carrick 1992). A minimum of 300 phytoplankton entities were enumerated under both high (1,000 to 1,200X) and low magnification (200X). Phytoplankton counts focused on non-flagellated forms and cells > 2 μm. Smaller cells and flagellates were more adequately enumerated with epifluorescent techniques outlined above. Cell volumes were estimated by determining average cell dimensions of a minimum of 100 cells for each dominant taxa and at least ten cells for rare taxa, and then applying these dimensions to appropriate geometric shapes. The cell volumes used for this study were from a compilation of values from this and previous studies in the Great Lakes. Phytoplankton volumes were converted to carbon units using the respective equations from Strathman (1967) for diatoms and Verity *et al.* (1992) for non-diatoms.

Rotifer samples were collected by filtering 8 to 20 L of raw water through a 30-μm screen and then washing the contents of the screen into a bottle. Rotifers and zebra mussel veligers were enumerated in a Sedgewick-Rafter cell under 100X magnification. A total of at least 60 rotifers was counted in each sample. Mean length for each taxa was determined for a minimum of ten randomly selected individuals. Rotifers were counted, sized, and converted to dry weight using the regression (for rotifers < 400 μm) of Stemberger and Gilbert (1987). Dry weights for zebra mussel veligers were assumed to be 0.1 μg (T. Nalepa, unpubl. data). Rotifer and veliger dry weights were converted to carbon using the factor 0.48 (Anderson and Hessen 1991).

Crustacean zooplankton abundance was determined by replicate metered net tows (0.5-m diameter, 153-μm mesh) from just below the bottom of the euphotic zone or from slightly above the bottom (western Lake Erie, E1; southern Lake Huron, H7) to the surface. Collections were taken almost exclusively during the night (primarily just before dawn). Comparisons of meter readings from meters located inside and outside the nets indicated high efficiency (> 90%) for all tows. The depth of the tows varied for each lake and were as follows: Lakes Michigan (M5-M6), Huron (H8-H9), and Ontario (O3-O4) = 0 to 40 m, Eastern Basin of Lake Erie (E2) and Southern Lake Huron (H7) = 0 to 30 m, Western Lake Erie (E1) = 0 to 7 m, and Lake Superior (S10-S12) = 0 to 50 m. For *Bythotrephes*, separate metered net tows with a 1-m 353-μm mesh net were performed during the summer of 1995. All zooplankton samples were narcotized and then preserved with sugar formalin (Haney and Hall 1973). The counting of crustacean zooplankton used the same technique as in several previous studies (Scavia *et al.* 1986, Bridgeman *et al.* 1995) and is described in Evans and Jude (1986). Briefly, each zooplankton sample was subsampled in order to give two samples of 150 to 200 organisms each. All cladocerans and adult copepods in each subsample were identified to species and sex. Immature copepodites were identified to genus, while nauplii were combined into one group. Mean length of each taxon was determined from a minimum of 20 randomly selected individuals of each taxon. Crustacean lengths (with the exception of *Bythotrephes*) were converted to dry weights using the regression of Culver *et al.* (1985). For *Bythotrephes*, the length-weight conversions of Berg and Garton (1988) were used. Crustacean dry weights were converted to carbon using the factor 0.48 (Anderson and Hessen 1991).

All of the plankton biomass data were normalized to carbon units. This decision was based on two factors: 1) carbon conversion factors are relatively robust and probably the most used biomass conversion factors (e.g., dry weight, wet weight) for microorganisms, and 2) carbon normalized data provide a common basis for assessing intercomparisons with the data collected in this study and to previously published work in the Great Lakes. The most appropriate carbon conversion values were used for all microorganism groups; they were internally consistent and sized-based both within all non-picoplankton groups and among all groups. For protozoans and other non-picoplankton, the conversion equations of Verity *et al.* (1992) for all non-diatoms and Strathman (1967) for all diatoms were used. The Strathman conversion factors are probably the most widely used and are similar to values from other studies (Cushing and Nicholson 1958, Parsons *et al.* 1961, Mullin *et al.* 1966). The Verity conversion factors provided consistency among all non-diatoms, and are relatively similar to those of Strathman (1967) and Moal *et al.* (1987). For prokaryotic picoplankton, the conversion factor of Lee and Fuhrman (1987) was used because it is similar to the value used for eukaryotic picoplank-

ton (0.38 vs. 0.36 pg/μm^3). This prokaryotic value also has independent support in the literature (Bratbak 1985, Borsheim and Bratbak 1987, Verity *et al.* 1992).

All biomass estimates from specific depths were depth-weighted and then averaged to produce a mean euphotic zone value. These mean euphotic zone values were used for all subsequent analyses. During the spring isothermal mixing period, these euphotic zone averages are similar to the surface mixed layer (ML) or water column averages; however, during summer stratification, they often differ considerably. Because of highly variable surface ML depths among years at the same station (often 3X), the euphotic zone averages are a more appropriate and reliable marker for making comparisons among stations. Moreover, surface ML depth can exhibit large changes with potentially 90% of its variability concentrated on less than daily time scales (McCormick and Meadows 1988). Parametric statistics were used to analyze differences among and between mean euphotic zone values (e.g., one-way ANOVAs for spatial differences, t-test for seasonal differences, etc.).

RESULTS

Baseline Limnological Conditions

The sampling periods during each year corresponded to spring isothermal mixing (late April/May) and summer stratification (August). With the exception of two samplings at Lake Michigan stations (M5 and M6) on 30 April 1993, all spring sampling occurred during the month of May. For spring 1993 and 1994, all stations (except western Lake Erie, E1) exhibited isothermal conditions with temperatures between 1° and 4°C. Sampling occurred two weeks later in May of 1995 than in 1993 and 1994, and slight stratification was found at two stations that were isothermal in previous years. Surface temperatures at the southern Lake Huron station (H7) and eastern basin of Lake Erie (E2) were 5°C, whereas all other stations in Lakes Huron, Michigan, and Ontario ranged between 2.5° and 4°C. The one station that consistently exhibited temperatures > 4°C during the May sampling was western Lake Erie; spring isothermal temperatures at that station ranged from 9° to 14°C for 1993 to 1995.

During the August sampling, surface temperatures in Lakes Michigan, Huron, and Ontario and in the eastern basin of Lake Erie ranged from 18° to 24°C. In western Lake Erie, surface temperatures ranged from 21° to 26°C. In Lake Superior, surface temperatures ranged from 7° to 11°C. The depth of the surface ML ranged from 6 to 20 m among all stations. Even at the same station, there was large variability in the depth of the ML among years. For example, at the eastern Lake Ontario station (O4), surface ML depth ranged from 6 m in 1994 to 18 m in 1993.

The depth of the euphotic zone was remarkably consistent among stations during the spring isothermal period (Table 1). With the exception of western Lake Erie (E1), all mean euphotic zone values ranged from 21 to 27 m. Shallow western Lake Erie was the only station that exhibited significant differences from other stations ($p < 0.05$). Summer euphotic zone values were more variable and distinguishable by lake (Table 1). Euphotic zone depths from stations in the lower lakes were smaller than those from upper lakes, while those from Lake Superior were larger than those from all other lakes ($p < 0.05$). Maximum euphotic zone depth values were similar for Lakes Huron, Michigan, Ontario, and the eastern basin of Lake Erie (Table 1). One interesting difference was that maximum values for stations in Lakes Huron and Michigan occurred in the summer, whereas maximum values for Lake Ontario and for the eastern basin of Lake Erie were found during the spring period. Western Lake Erie had similar values for both seasons.

Spring total P concentrations averaged over the euphotic zone were remarkably consistent among stations, particularly Lakes Michigan and Ontario (Table 1). Overall, Lake Huron P concentrations were lowest, followed by a group of stations from Lakes Michigan, Ontario, and the eastern basin of Lake Erie, and then the western Lake Erie station. However, statistically significant differences were associated only with the western Lake Erie station ($p < 0.05$). Summer total P concentrations averaged over the euphotic zone were also consistent, particularly for the upper lakes (Table 1). In general, P concentrations in the lower lakes were higher than those in the upper lakes. Highest values were found for western Lake Erie, which were significantly different from all stations with the exception of the western basin of Lake Ontario ($p < 0.05$). Values from Lakes Michigan, Huron, and Superior were relatively similar ($p > 0.05$).

Autotrophic Plankton Community

Due to the low sampling frequency, this work focused on spatial (stations) and seasonal (spring vs.

summer) comparisons by combining data from all 3 years (1993 to 1995). With only three years of sampling and only one sampling per season at each station, it was not feasible to assess both seasonal and annual temporal scales. Combining annual data (three samplings per station during each season) permits examination of mean values for stations and seasons. Moreover, the focus on spatial and seasonal data was reasonable given the uniqueness of sampling in all five lakes and previous information on structural differences between spring and summer planktonic food-webs in the Great Lakes (Scavia and Fahnenstiel 1987). A preliminary comparison of the data supported our seasonal emphasis; of the seventeen ratios analyzed in this study (e.g., autotrophic:heterotrophic, picoplankton: nanno- and microplankton, etc.) fifteen exhibited significant differences between the seasons ($p < 0.05$).

Euphotic zone total autotrophic biomass ranged from 23 mg C/L to 128 mg/L (Fig. 2). In general, autotrophic biomass was higher during summer stratification (40 vs. 76, $p < 0.05$) for all stations except southern Lake Michigan (M1). Mean spring phytoplankton was relatively similar among stations, ranging from 28 mg C/L at O4 to 57 mg C/L at E1 ($p > 0.05$; Fig. 2a). Mean summer phytoplankton biomass was more variable, ranging from 23 mg C/L at S12 to 128 mg C/L at E1. Lake Superior stations (S10, S11, S12) exhibited the lowest biomass, while western Lake Erie (E1) and eastern Lake Ontario (O4) exhibited the highest (Fig. 2b).

Two components of the autotrophic community were analyzed based on size (Fig. 2); picoplankton (organisms < 2 μm) and all larger autotrophs. The contribution of autotrophic picoplankton varied seasonally ($p < 0.05$), but not among stations for either season ($p > 0.05$). In the spring period, picoplankton accounted for only 10% (range of station means, 2 to 19%) of total autotrophic biomass whereas during summer stratification, picoplankton accounted for 32% (range in station means, 18 to 58%). The greatest contribution of picoplankton to total autotrophic biomass was found in Lake Superior (51 to 58%). Seasonal differences were most pronounced in the lower lakes (Lakes Erie and Ontario), where picoplankton biomass increased 11 to 23-fold from spring to summer (Fig. 2). In Lakes Huron and Michigan, picoplankton biomass increased 2.8 to 4.0-fold from spring to summer.

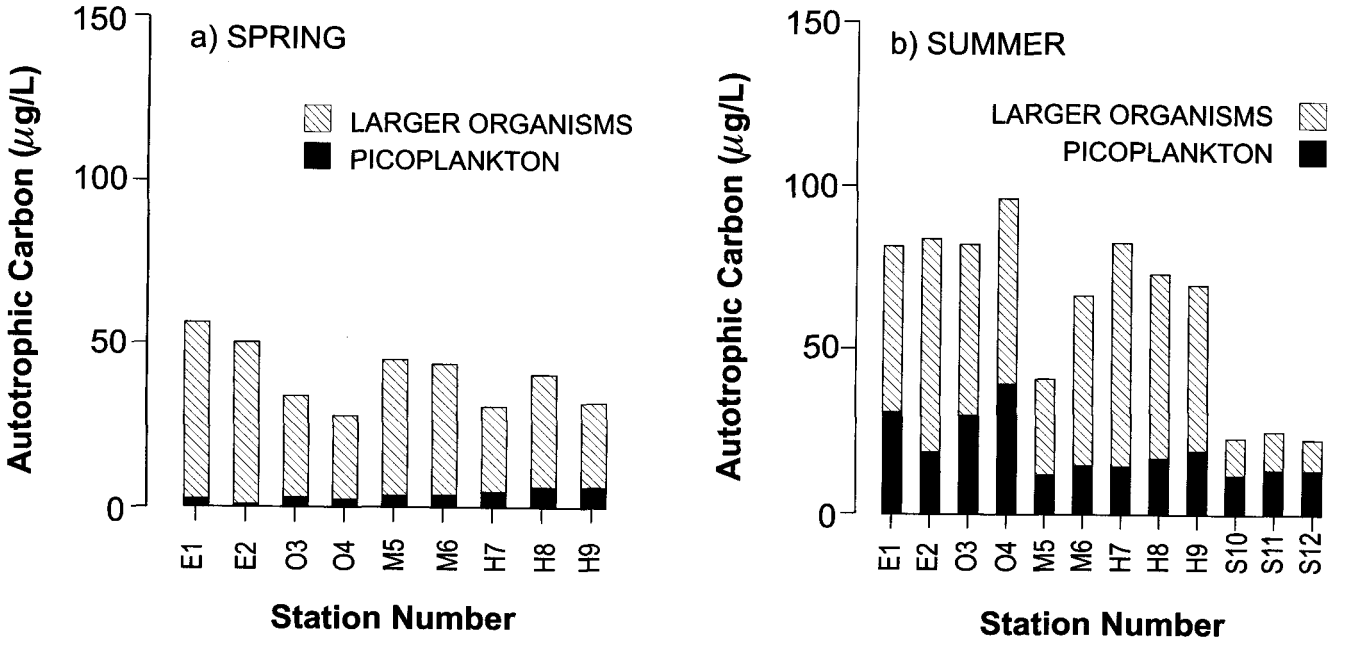

FIG. 2. Autotrophic carbon of picoplankton (< 2 μm) and larger-sized organisms for each sampling station during a) spring and b) summer sampling periods. Specific information on station locations and abbreviations can be found in Figure 1 and Table 1.

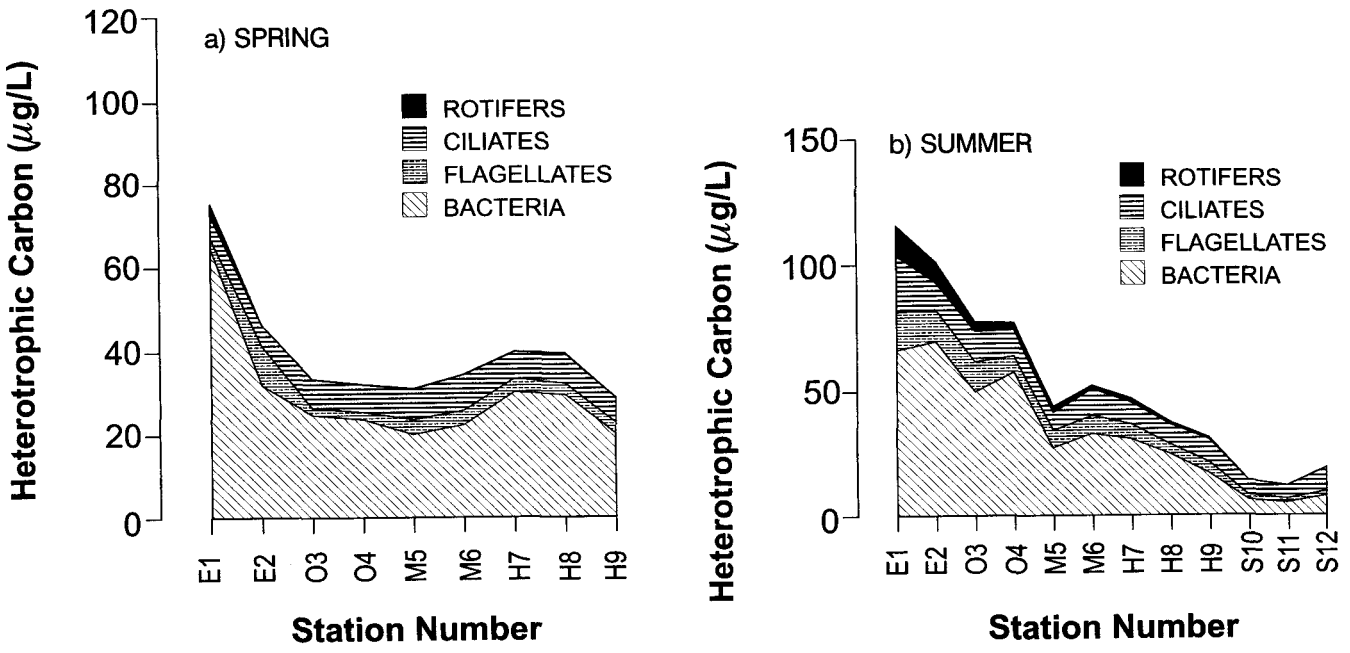

FIG. 3. Carbon concentration of major groups of heterotrophic microorganisms for each sampling station during a) spring and b) summer sampling periods. Specific information on station locations and abbreviations can be found in Figure 1 and Table 1.

Heterotrophic Microorganisms

Taxonomic affinity was used to distinguish microorganisms. Microorganisms are defined as all autotrophic organisms and all heterotrophic organisms with the exception of crustaceans. Heterotrophic microorganisms include bacteria, protozoans, rotifers, and zebra mussel veligers. This taxonomic grouping also has size differentiation. The largest heterotrophic microorganism, the rotifer *Conochilus unicornis*, had a mean length of 285 μm whereas the smallest crustaceans, copepod nauplii, had mean lengths ranging from 279 to 323 μm. Further justification for this distinction comes from sample collection. All samples for microorganisms were collected from discrete water samples. Crustaceans were collected from integrating net tows.

Total heterotrophic microorganism biomass in the euphotic zone ranged from 12 to 116 μg C/L. Summer biomass was higher than spring biomass (Fig. 3; means = 40 μg C/L and 60 μg C/L, $p < 0.05$). During spring, biomass was relatively consistent among stations with the exception of western Lake Erie (E1) (Fig. 3a; $p < 0.05$ for all stations except E6). During summer, a consistent trend of increasing biomass was found among lakes in the order of Lakes Superior, Huron, Michigan, Ontario, and Erie (Fig. 3b).

The structure of the heterotrophic microorganism community was remarkably similar among lakes, especially during the spring isothermal period (Figs. 3 and 4). Significant seasonal differences in the relative contribution to total biomass were noted for all major groups (bacteria, protozoans, and rotifers, $p < 0.05$); however, with the exception of protozoans during the summer, no statistically significant differences were noted for any major groups among stations within either season. Bacteria constituted 72% of total heterotrophic microorganism biomass during the spring isothermal period and 60% during summer (Fig. 4).

Heterotrophic protozoans (ciliates and flagellates) were another important group of heterotrophic microorganisms (Figs. 3 and 4), comprising 32% of total heterotrophic microorganism biomass. The contribution of protozoans varied with season ($p < 0.05$). Unlike bacteria, the greatest contribution of protozoans occurred in summer (36%) as compared to spring (28%). In the spring, the relative contribution ranged from 13 to 36% with the lowest value from western Lake Erie (Fig. 4a). During the summer, the relative contribution varied signifi-

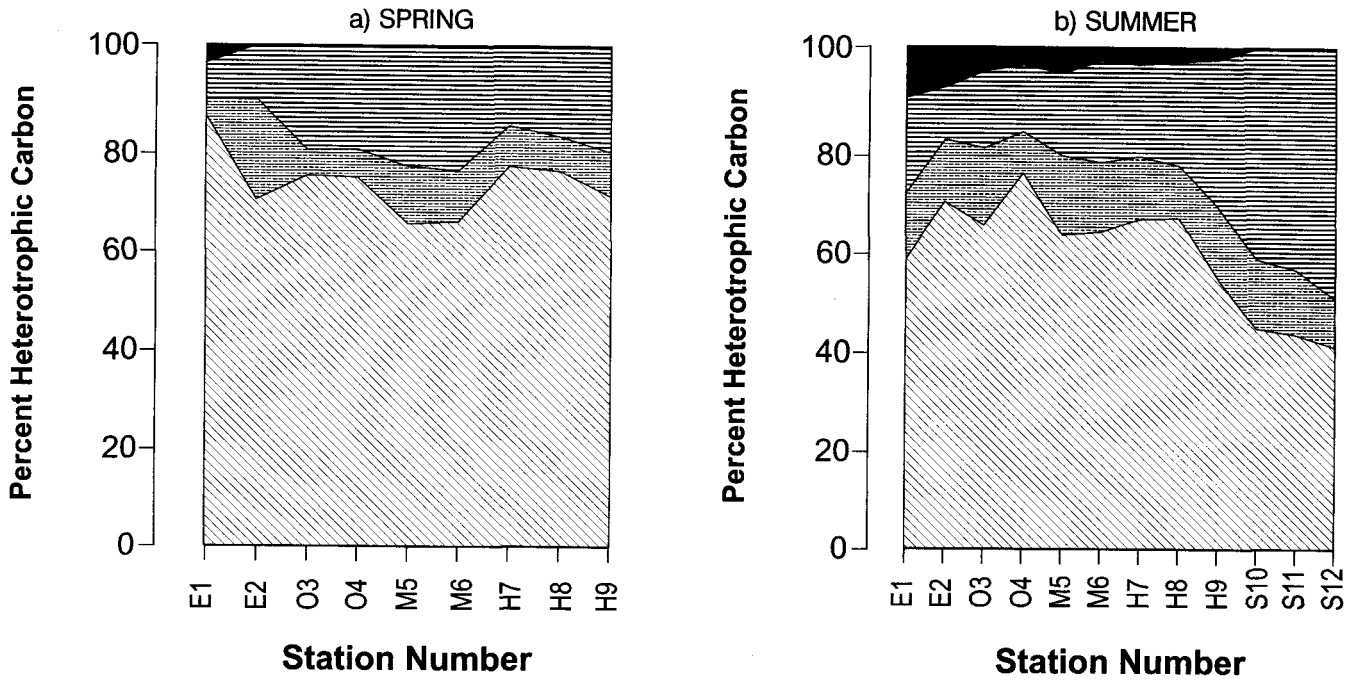

FIG. 4. The percent contribution of bacteria = ▨, flagellates = ▤, ciliates = ▤, and rotifers = ■ to total heterotrophic microorganism carbon concentration for each sampling station during a) spring and b) summer sampling periods. Specific information on station locations and abbreviations can be found in Figure 1 and Table 1.

cantly by station (Fig. 4b; $p < 0.05$). The largest contributions, > 55% to total heterotrophic microorganism biomass, were found in Lake Superior. All other stations had values between 26 and 44%. Heterotrophic protozoans were composed of two groups, flagellates and ciliates. Ciliates were the dominant group, comprising 64% of total heterotrophic protozoan biomass. Their contribution was relatively consistent for both spring and summer sampling periods, 68 and 61%, respectively. Station values ranged from 60 to 84% with the exception of the eastern basin of Lake Erie (E2, 42%).

Rotifers were a minor component of the heterotrophic microorganism community (mean contribution, 2.6%; Figs. 3 and 4). During the spring period when the mean rotifer contribution was < 1% , individual station mean values ranged from < 0.1% to 2.6% (Fig. 4a). Rotifer contribution increased significantly ($p < 0.05$) during the summer stratification, when they constituted 4.5% of total biomass (Fig. 4b). Even though station-specific values varied from a low of < 1% at Lake Superior stations to > 10% in western Lake Erie, no statistically significant differences were noted among stations (Fig. 4; $p > 0.05$).

Even though zebra mussel veligers were found in all lakes except Lake Superior, their contribution to heterotrophic microorganism biomass never exceeded 1% on any occasion. During summer when they were most abundant, their mean contribution to heterotrophic microorganism biomass was 0.1%. Because they are only planktonic during a specific part of their life cycle and because their biomass was so low, they were not included in any further analyses.

Structure of Microorganism Food-Web

Total microorganism biomass varied from 37 µg/L at a station in Lake Superior (S11) to 243 µg/L at the western Lake Erie station (E1). Mean biomass was higher during summer than during the spring sampling ($p < 0.05$, summer = 135 µg/L, spring = 80 µg/L). A significant relationship existed between total phosphorus concentration and total microorganism biomass, whether all data or just station mean values were used ($p < 0.05$, $y = 9x + 48.3$, $r^2 = 0.41$, $n = 55$ all data; $p < 0.05$, $y = 12.1x$

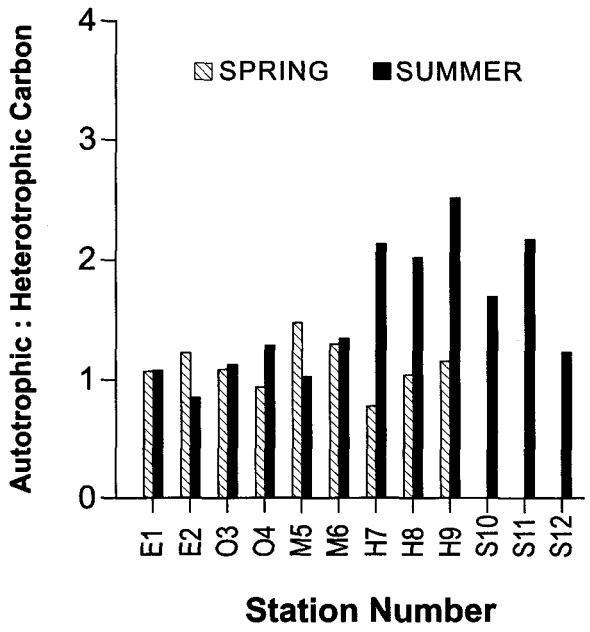

FIG. 5. Ratio of autotrophic:heterotrophic carbon for microorganisms for each sampling station during spring and summer sampling periods. Specific information on station locations and abbreviations can be found in Figure 1 and Table 1.

+ 25.7, $r^2 = 0.63$, n = 20, station means from each season). The limited range of total phosphorus concentrations from Lakes Huron, Michigan, Superior, and Ontario has an effect of overleveraging the higher values from western Lake Erie.

For microorganisms, the ratio of autotrophic to heterotrophic biomass averaged 1.3 (Fig. 5). Significant differences were noted by season ($p < 0.05$). During the spring period, the ratio averaged 1.1, whereas it increased to 1.5 during summer (Fig. 5). Mean ratios for stations during the spring period were similar ($p > 0.05$), ranging from 0.78 to 1.47. The increase in the mean summer value was attributable to higher values in Lakes Huron and Superior, where the summer mean value of 2.1 was significantly higher than summer mean values for Lakes Michigan, Erie, and Ontario ($p < 0.05$, mean = 1.1, Fig. 5). In Lakes Michigan, Erie, and Ontario, mean station ratios, ranging from 0.8 to 1.3, were similar among stations and between seasons ($p > 0.05$).

We took a simple functional approach to the microorganism community by examining the biomass of producers (autotrophs), decomposers (heterotrophic bacteria), and micrograzers (heterotrophic protozoans and rotifers) (Fig. 6). Produc-

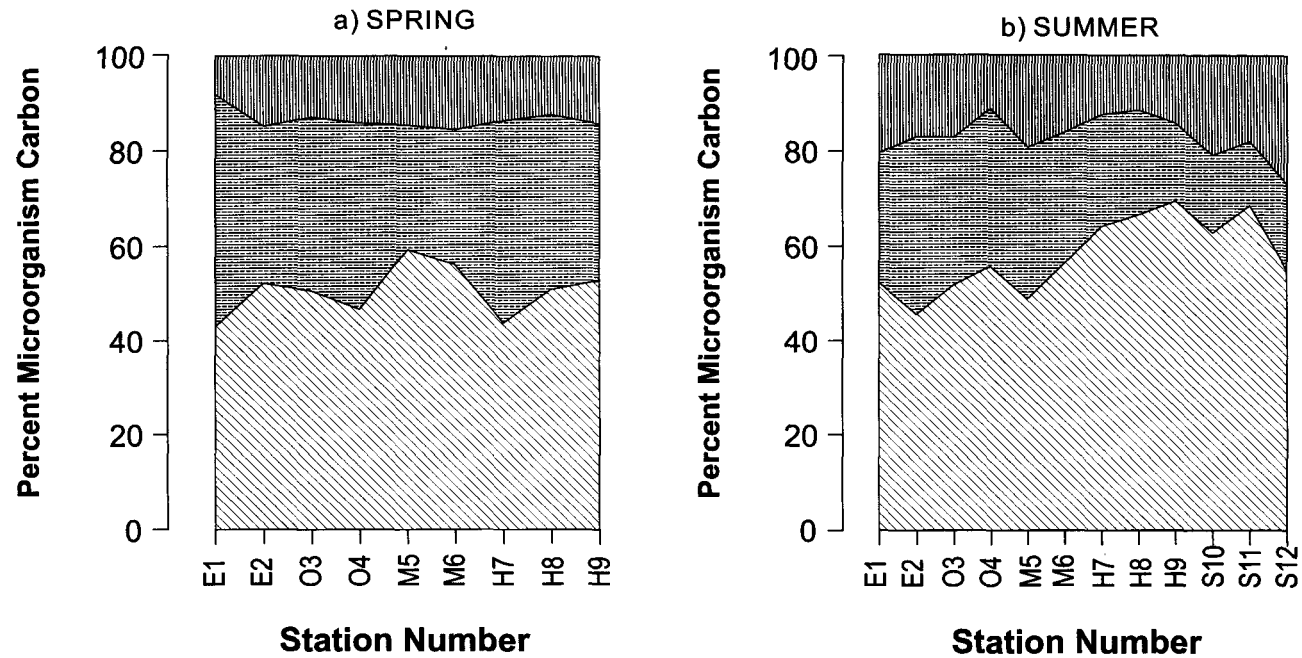

FIG. 6. Percent contribution of producers (▨, autotrophs), decomposers (▤, heterotrophic bacteria), and micrograzers (▥, heterotrophic protozoans and rotifers) to total microorganism carbon for each sampling station during a) spring and b) summer sampling periods. Specific information on station locations and abbreviations can be found in Figure 1 and Table 1.

ers, decomposers, and micrograzers composed on average 54%, 31%, and 15% of total biomass, respectively. The relative contribution of all groups varied seasonally ($p < 0.05$), but limited variation was noted among stations within a season. During spring, the contribution of autotrophs, bacteria, and micrograzers was relatively similar among stations ($p > 0.05$) and averaged 50% (station range 42 to 56%), 37% (station range 30 to 43%), and 13% (station range 8 to 16%), respectively (Fig. 6a). During the summer, however, the relative contribution among groups was more variable (Fig. 6b). Significant differences among stations were noted for autotrophs ($p < 0.05$), but not for bacteria or micrograzers ($p > 0.05$). Autotrophs were greater contributors to total biomass in Lakes Huron and Superior than in Lakes Erie, Michigan, and Ontario ($p < 0.05$, mean Superior and Huron values = 64% , mean Erie, Ontario, and Michigan values = 52%). Overall, the contribution of autotrophs, bacteria, and micrograzers for the summer sampling period averaged 57%, 26%, and 17% , respectively.

For size analysis we used the definitions of Sieburth *et al.* (1978) and maximum linear dimensions to classify microorganisms as picoplankton (0.2 to 2 μm) or nanno- and microplankton (2 to 200 μm). The ratio of picoplankton biomass to total nanno- and microplankton biomass averaged 0.96 (Fig. 7). No significant differences were found in the ratio of picoplankton to total nanno- and microplankton between seasons (spring = 1.0, summer 0.91) or among stations within a season ($p > 0.05$ in all cases).

Crustaceans

The final component of the planktonic food-web is the mesograzers or crustaceans. Due to their size and biology, crustacean zooplankton occupied a unique position in this investigation, and our data on their abundance is the least consistent with data collected for all other groups. Because of their size, crustaceans were collected with nets, whereas all other components were collected from the same discrete water samples. At all stations, crustacean biomass was much greater during summer stratification than during spring (Fig. 8; $p < 0.05$, spring mean = 18 μg /L, summer mean = 107 μg/L). During the spring, significant differences were noted among stations ($p < 0.05$). Mean values from Lakes Huron and Michigan were significantly larger than values from Lakes Erie and Ontario ($p < 0.05$, mean Huron and Michigan = 27 μg/L, mean Erie and Ontario = 8 μg/L). Not only did total crustacean biomass increase during the summer, but the variability among stations did as well (Fig. 8). Crustacean biomass increased in order from Lakes Superior (28 μg/L), Huron (79 μg/L), Ontario (112

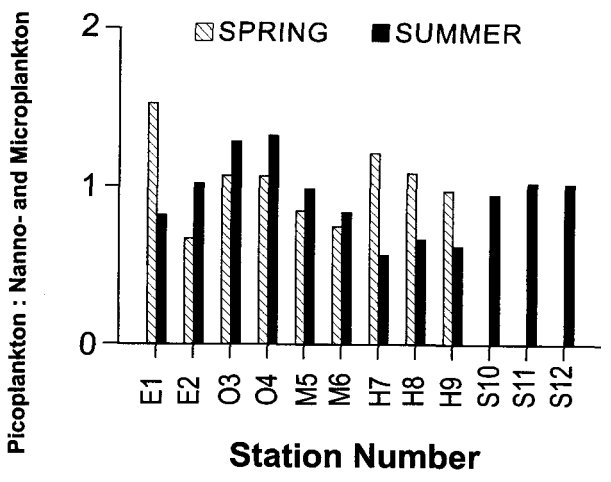

FIG. 7. Ratio of picoplankton carbon : nanno- and microplankton carbon for each sampling station during spring and summer sampling periods. Specific information on station locations and abbreviations can be found in Figure 1 and Table 1.

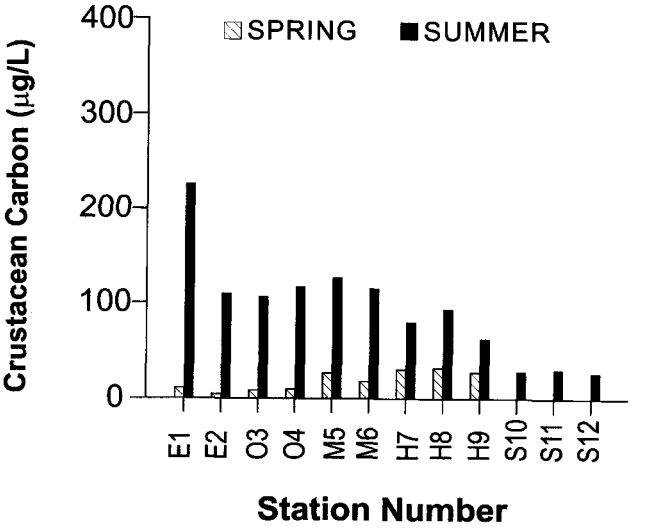

FIG. 8. Crustacean carbon for each sampling station during spring and summer sampling periods. Specific information on station locations and abbreviations can be found in Figure 1 and Table 1.

µg/L), Michigan (120 µg/L), and Erie (168 µg/L) (Fig. 8). The most variability between stations in the same lakes was found in Lake Erie, where western (E1) and eastern (E2) portions of the lake varied by a factor of 2.1.

Structure of Planktonic Food-Web

All further analysis will consist of all planktonic organisms including crustaceans. The ratio of autotrophic biomass to total heterotrophic biomass was strongly influenced by crustacean biomass, as these ratios were much lower than the ratio for microorganisms (Fig. 9). The mean ratio of autotrophic: heterotrophic biomass from spring (0.73) was significantly higher than the summer ratio (0.51; $p < 0.05$). During the spring, the mean ratio was relatively similar among stations ($p > 0.05$), ranging from 0.5 to 1.0. During summer stratification, mean values at most stations were lower with the exception of the Lake Huron stations (Fig. 9). Mean values from most stations also were relatively similar, ranging from 0.38 to 0.61, with the exception of all Lake Huron stations (H7-H9, mean = 0.69) which were significantly higher than the others ($p < 0.05$) and the southern Lake Michigan station (M5, mean =0.25) which was significantly lower ($p < 0.05$). The low values from the Lake Michigan station can be attributed to the large summertime crustacean component; crustacean biomass in Lake Huron was approximately half that of Lake Michigan (Fig. 8).

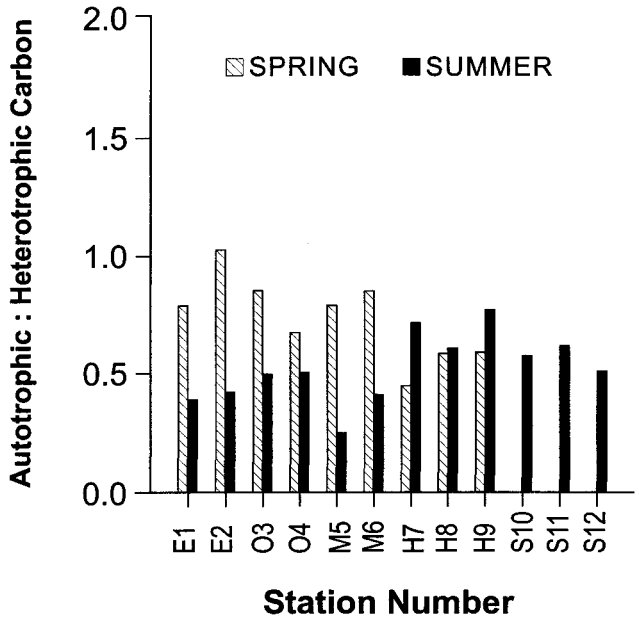

FIG. 9. Ratio of autotrophic:heterotrophic carbon for all planktonic organisms during spring and summer sampling periods. Specific information on station locations and abbreviations can be found in Figure 1 and Table 1.

For these analyses, the planktonic food-web was divided into major functional groups; producers (autotrophs), decomposers (heterotrophic bacteria), micrograzers (heterotrophic protozoans, rotifers, and veligers), and mesograzers (crustaceans). Because of the large increase in mesograzers during summer stratification, both absolute values (Fig. 10) and relative values (Fig. 11 and discussion) are presented. With the exception of micrograzers, all major groups exhibited significant seasonal differences ($p < 0.05$) in their relative contribution to total planktonic biomass. During the spring period, the percent contributions of autotrophs, decomposers, micrograzers, and mesograzers were 40%, 30%, 11%, and 19%, respectively. The only significant difference among stations in the relative contribution of any major group to total planktonic biomass was the larger contribution of mesograzers (26%) in Lakes Huron and Michigan as compared to Lakes Erie and Ontario (9%; $p < 0.05$; Fig. 10a). During summer stratification, the autotrophs, decomposers, micrograzers, and mesograzers constituted 32%, 15%, 9%, and 44% of total plankton biomass, respectively. Although there were no significant differences in the relative contribution of all major groups among stations ($p > 0.05$), the relative contribution of mesograzers was notably higher for Lake Michigan than for all other lakes (Fig. 10b). Mesograzers constituted 54% of the total biomass in Lake Michigan and 41% in the other four lakes.

The structure of the entire planktonic food-web was also analyzed by size by adding mesoplankton (organisms 200 to 20,000 µm) to the picoplankton (0.2 to 2.0 µm) and nanno- and microplankton (2 to 200 µm) groups already presented. Overall, picoplankton, nanno- and microplankton, and mesoplankton constituted 29%, 33%, and 37% of total plankton biomass (Fig. 12). The contribution of all three groups exhibited significant differences by season ($p < 0.05$, Fig. 12). The mesoplankton increased in relative contribution from spring to summer (spring = 28%, summer = 46%) whereas picoplankton and nanno- and microplankton exhibited a decrease (spring, pico. = 34%, nanno. and micro. = 38%; summer, pico. = 25%, nanno. and micro. = 29%). No significant differences were

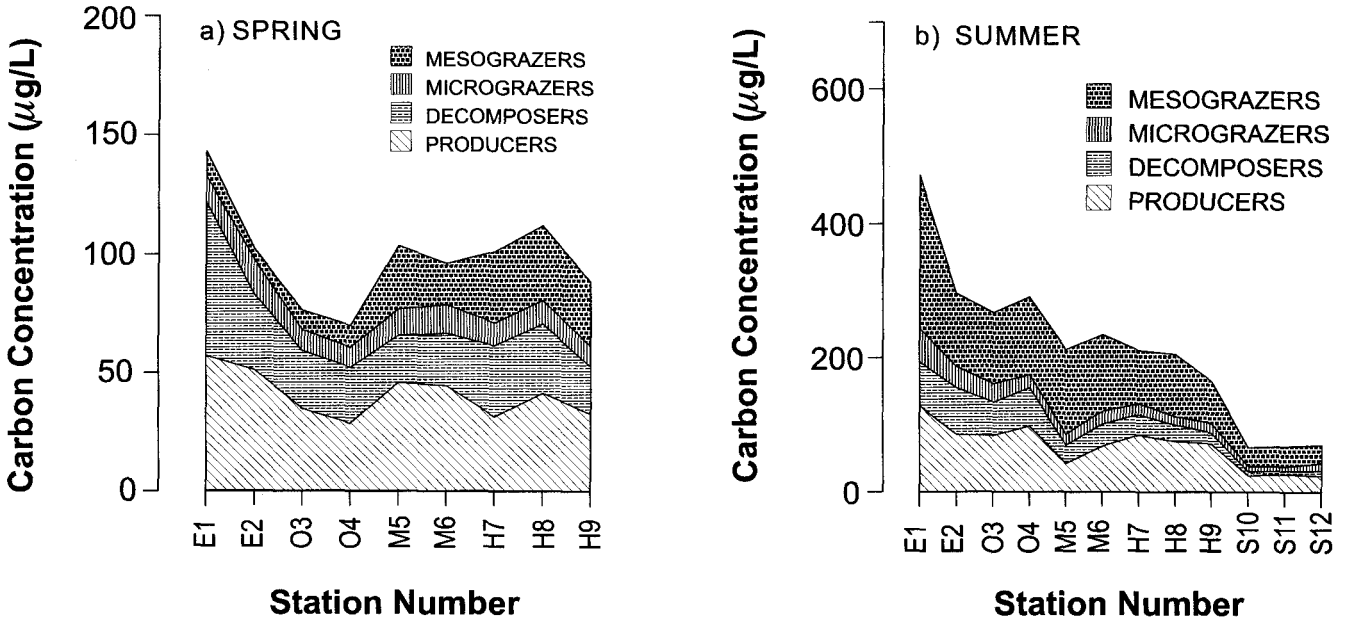

FIG. 10. Planktonic carbon of producers (autotrophs), decomposers (heterotrophic bacteria), micrograzers (protozoans and rotifers), and mesograzers (crustaceans) during a) spring and b) summer sampling periods for each sampling station. Specific information on station locations and abbreviations can be found in Figure 1 and Table 1.

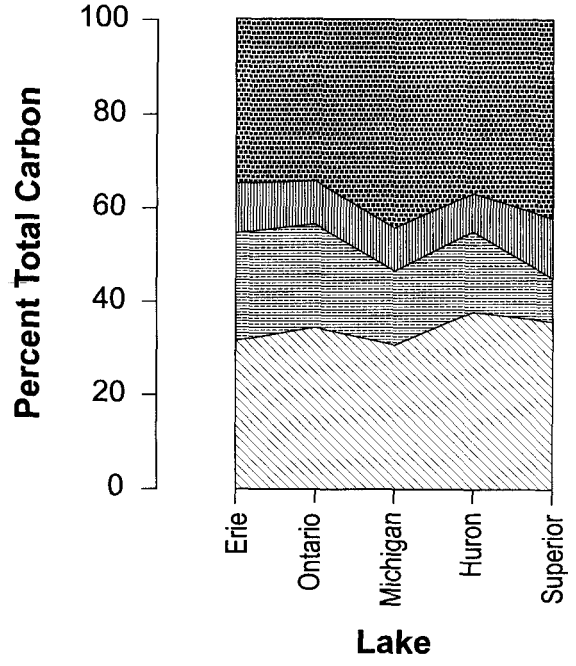

FIG. 11. Percent contribution of producers (▨, autotrophs), decomposers (▤, heterotrophic bacteria), micrograzers (▥, protozoans and rotifers), and mesograzers (▦, crustaceans) to total plankton carbon for each Great Lake.

noted among stations within a season for any of the groups ($p > 0.05$) with the exception of mesoplankton in the spring. The contribution of mesoplankton in Lake Erie (14%) was lower than those in Lakes Huron (37%) and Michigan (35%).

DISCUSSION

Planktonic Food-Web Structure

This study represents the first attempt to characterize the entire planktonic food-web in all five St. Lawrence Great Lakes using the same techniques, and for the microplankton, the same water sample. As such, many insights into relative community structure should be provided that hitherto have been impossible. Previous descriptive work on the structure of the Great Lakes planktonic food-web has been more restrictive, e.g, confined to a specific taxonomic group or spatial area (e.g., Vollenweider *et al.* 1974, Watson 1974, Munawar and Munawar 1986, Lean *et al.* 1987, Scavia and Fahnenstiel 1987, Sprules *et al.* 1991, Johannsson *et al.* 1991). Many of these studies focused on the lowest level of organization (species) within broad taxonomic groups, i.e., ciliates, phytoplankton, rotifers, and consequently differences in community structure

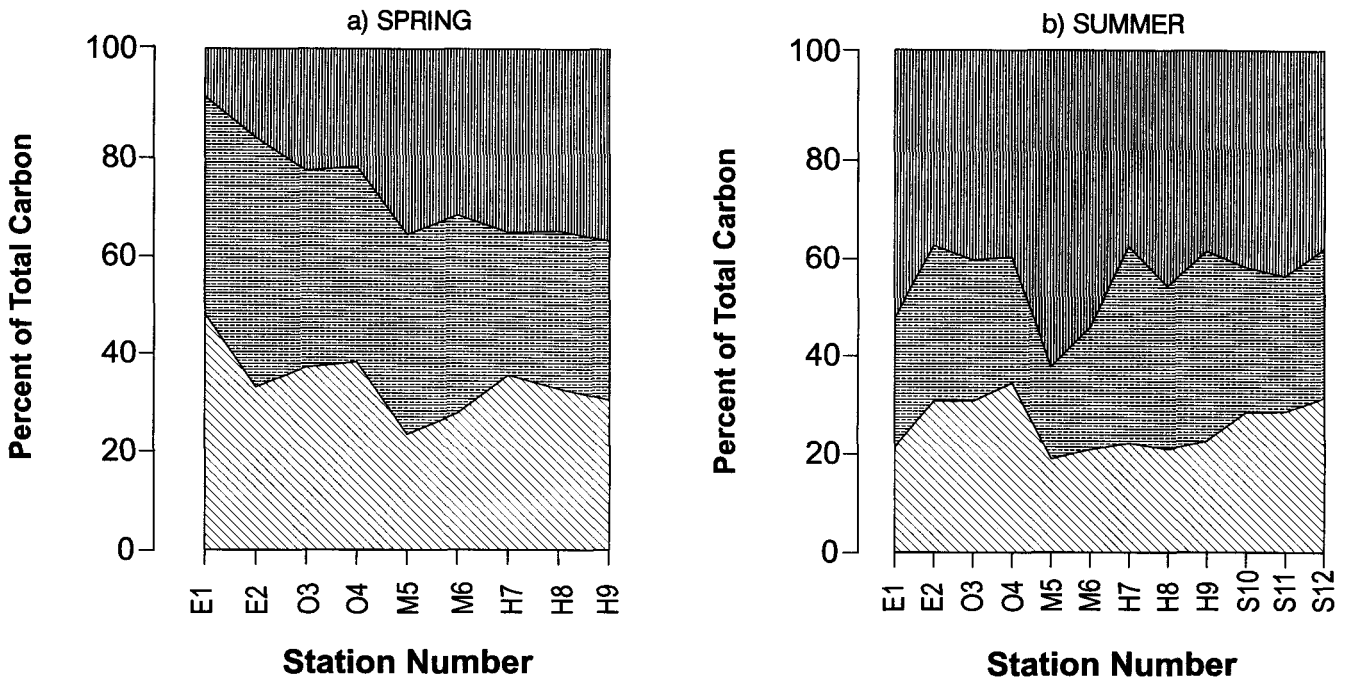

FIG. 12. Percent contribution of picoplankton (▨), nanno- and microplankton (▤) and mesoplankton (▦) to total planktonic carbon for each sampling station during the a) spring and b) summer sampling periods. Specific information on station locations and abbreviations can be found in Figure 1 and Table 1.

were emphasized. While species differences within broad taxonomic groups were also found and will be discussed in future studies, the patterns elucidated in this study were only possible by analyzing all components microscopically to the lowest taxonomic level (in most cases, species) using appropriate techniques, expressing all biomass in similar units, and focusing on broad taxonomic, functional, or size groups.

Despite the limited sampling during two major thermal periods in this study, the similarity in the structure of the planktonic food-web, as evidenced by the relative contribution of broad taxonomic, functional or size groups (Figs. 4, 6, 10, and 12) among all stations in the Great Lakes, was remarkable and surprising. Although the absolute biomass of major groups varied in some cases by a factor of ten among stations (Figs. 3 and 10), variation in relative contribution was far more constrained (usually less than a factor of two) and predictable. Most of the variation in structure was noted between seasons and not spatially within or among stations in different lakes. Of the seventeen ratios analyzed in this study (e.g., bacteria:total microheterotrophs, picoplankton:nanno- and microplankton, autotroph:heterotroph), fifteen varied significantly between seasons. However, during the spring only two parameters varied significantly among stations, and during summer only four parameters varied significantly among stations. Given the limited sampling and previous literature noting differences in the planktonic food-web among lakes at lower levels of organization, this much similarity among stations was not anticipated.

The broad similarity in the structure of the microorganism community across the offshore regions of the Great Lakes appears to be a relatively recent phenomenon, likely due to recent changes in the structure of the community in the lower lakes. Although data are limited, previous studies from Lakes Michigan, Huron, and Ontario provide for a provisional comparison to conditions in the 1980s. These comparisons are limited to studies of broad taxonomic groups including the abundance and biomass of microorganisms in Lakes Michigan and Huron in the late 1980s (Scavia *et al.* 1986, Makarewicz 1987, Carrick and Fahnenstiel 1989, Pernie *et al.* 1990, Carrick and Fahnenstiel 1990, Fahnenstiel and Carrick 1992). The comparisons are limited to previous studies that sampled the off-

shore regions of these lakes during similar time periods and utilized similar techniques. Results from these studies suggest that the structure of the microorganism community has not changed in Lakes Michigan and Huron from the late 1980s through the early/mid 1990s as abundances of all major groups were similar between the two time periods (Table 2).

Unlike Lakes Michigan and Huron, the structure of the microorganism community in Lake Ontario, and possibly Lake Erie, appears to have changed from the 1980s (Table 2). Results of a large interdisciplinary study of the Lake Ontario food-web, conducted in 1982 as part of the Lake Ontario Nutrient Assessment Study (LONAS), were reported in several papers (Gray 1987, Pick and Caron 1987, Taylor *et al.* 1987, Taylor and Heynen 1987, Mazumder *et al.* 1992). Lean *et al.* (1987) summarized most of the results, expressing all values in similar units and the results from the mid-lake station (403) are presented in Table 2. Bacteria and phytoplankton biomass in the 1993 to 1995 period were approximately half of 1982 values; however, ciliate biomass was relatively similar for the two periods (Table 2). Rotifers exhibited the most pronounced difference between the two time periods (Table 2). In 1982, rotifers constituted over 75% of total zooplankton biomass with rotifers biomass values of approximately 82 μg C/L during the July/August period. Summer rotifer biomass values for Lake Ontario in this study averaged only 3.3 μg C/L and the highest value was only 4.8 μg C/L. The higher values for rotifers in 1982 even exceeded the 1993 to 1995 estimates of total heterotrophic microorganism biomass (bacteria, protozoans, and rotifers), which averaged 77 μg C/L. The high values reported by Mazumder *et al.* (1992) are not consistent with estimates from Haney grazing chambers reported by Taylor *et al.* (1987) from the same study period. Their rotifer biomass averaged approximately 12 μg C/L which are more consistent with the numbers reported in this investigation.

Autotrophic:heterotrophic ratios for the plankton communities in the Great Lakes may be useful for assessing the status or health of the system. Average autotrophic/heterotrophic ratios for microorganisms and for all plankton for the Great Lakes were 1.3 and 0.6, respectively (Figs. 5 and 9). The overall autotrophic:heterotrophic ratio (all plankton) is much lower than the microorganism ratio, due to the inclusion of crustaceans. While this total plankton ratio is interesting and useful for future comparisons, it has limited value in assessing ecosystem function or status. For microorganisms, the size and generation times of autotrophs and heterotrophs are relatively similar, whereas crustaceans are much larger than the other groups and typically exhibit much longer generations. This longevity allows them to better integrate environmental variability, but provides for a less direct coupling with present microplankton populations and environmental conditions.

An interesting aspect of the autotrophic:heterotrophic ratios is the limits or constraints on variability and the role of self-regulating mechanisms on these ratios. The relationship between this variability and the controlling influence of abiotic and biotic perturbations is of particular interest for the Great Lakes. These relationships are interesting not only as they apply to broad functional ratios, but to all aspects of broad food-web structure discussed in this paper. Food-web structure appears to control the energy transfer within the food-web, and therefore ultimately, overall trophic efficiency (Hairston and Hairston 1993). Thus, the limits to variation and constraints of the planktonic food-web structure will likely have implications for management of the Great Lakes. However, without a larger number of observations over a greater range of conditions, it is difficult to adequately address questions of limits and control of variability. The present study begins this process, as some interesting patterns were noted. For example, microorganism autotrophic:heterotrophic ratios were significantly higher during the summer in Lakes Huron and Superior as compared to the other lakes which might suggest some possible link between these ratios and the degree of anthropogenic alteration. Also, microorganism autotrophic:heterotrophic ratios might be expected to decrease during the summer as compared to the spring because some heterotrophic growth rates appear to be inhibited at lower temperatures (Scavia and Laird 1987); however the opposite was found. Total autotrophic:heterotrophic ratios did exhibit this seasonal pattern, but this was related to the large increase in crustacean biomass during the summer.

Abiotic and Biotic Control of Food-Web Structure

One important environmental factor that changed from the 1980s to the 1990s in Lakes Ontario and Erie, and likely played a role in controlling the abundance and composition of the microorganism communities, was the availability of phosphorus.

TABLE 2. Comparison of microorganism biomass in the offshore regions of Lakes Huron, Michigan and Ontario from the 1980s to 1993–1995. Mean abundance (mg C/L) for each major group is presented.

Lake	Parameter	Sampling Period	Mean Value	Reference
Michigan	Autotrophs	April–October 1986–1988	50	Fahnenstiel and Carrick 1992
Michigan	Autotrophs	April/May and Aug. 1993–1995	50	This study
Michigan	Heter. bacteria	April/May and Aug. 1985–1987	27	Pernie *et al.* 1990[1]
Michigan	Heter. bacteria	April/May and Aug. 1993–1995	26	This study
Michigan	Heter. flagellates	May and August 1987	13	Carrick and Fahnenstiel 1989
Michigan	Heter. flagellates	April/May and Aug. 1989	5	Carrick *et al.* 1991
Michigan	Heter. flagellates	April/May and Aug. 1993–1995	6	This study
Michigan	Ciliates	April–September 1987	9	Carrick and Fahnenstiel 1990[2]
Michigan	Ciliates	April/May and August 1989	4	Carrick *et al.* 1991
Michigan	Ciliates	April/May and Aug. 1993–1995	8	This study
Michigan	Rotifers	April/May and August 1984	0.6	Makarewicz 1987[3]
Michigan	Rotifers	April/May and Aug. 1993–1995	0.9	This study
Huron	Autotrophs	April–October 1986–1988	41	Fahnenstiel and Carrick 1992
Huron	Autotrophs	May and August 1993–1995	55	This study
Huron	Heter. flagellates	May and August 1987	10	Carrick and Fahnenstiel 1989
Huron	Heter. flagellates	May and August 1993–1995	4	This study
Huron	Ciliates	May and August 1987	7	Carrick and Fahnenstiel 1990[2]
Huron	Ciliates	May and August 1993–1995	7	This study
Huron	Rotifers	May and August 1984	0.5	Makarewicz 1987[3]
Huron	Rotifers	May and August 1993–1995	0.6	This study
Ontario	Autotrophs	August 1982	236	Lean *et al.*1987[4]
Ontario	Autotrophs	August 1993–1995	90	This study
Ontario	Bacteria	August 1982	108	Lean *et al.* 1987[4]
Ontario	Bacteria	August 1993–1995	54	This study
Ontario	Ciliates	August 1982	14	Lean *et al.* 1987[4]
Ontario	Ciliates	August 1993–1995	11	This study
Ontario	Rotifers	August 1982; July/August 1982[5]	196, 82	Mazumder *et al.* 1992[3]
Ontario	Rotifers	August 1982	12	Taylor *et al.* 1987[3]
Ontario	Rotifers	August 1993–1995	3	This study

[1]Bacteria abundance was converted to carbon using biovolume conversion factor from Scavia *et al.* 1986 and carbon conversion factor of 0.38 pg C/μm.
[2]Ciliate wet weight was converted to carbon assuming a specific weight of 1 g/mL and a 0.2 pg C/μm conversion factor.
[3]Dry weight was converted to carbon using 0.48 μg C/μg dry weight conversion factor.
[4] Wet weight was converted to carbon assuming a specific weight of 1g/mL and carbon conversion factors of 0.2 pg C/μm for phytoplankton and ciliates and 0.38 pg C/μm for bacteria. All data taken from station # 403.
[5] The most appropriate comparison would be August to August; however one high value was found in August so we also calculated a July/August mean with the high August value excluded.

Total phosphorus concentrations exhibited a large decrease from 1980 through the 1990s due to decreased phosphorus loading and the impacts of non-indigenous mussels (*Dreissena polymorpha*, and possibly *D. bugensis*). Phosphorus loadings to Lake Ontario decreased substantially in the 1970s producing large decreases in lake concentrations by the 1980s (Johengen *et al.* 1994). Total phosphorus concentrations decreased from 16 μg/L in 1981 to 10 μg/L in 1991. The changes in phytoplankton biomass from the 1982 and 1993 to 1995 studies (Table 2) are consistent with the decline in phosphorus concentrations. The significant relationship between total phosphorus concentrations and microorganism biomass in this study ($r^2 > 0.40$) supports the primary role of phosphorus in controlling planktonic biomass. Despite no further declines in phosphorus loadings in the 1990s (J. Hartig, IJC, pers. comm.) these data suggest that offshore phosphorus concentrations have declined further in Lake Ontario in 1993 to 1995 (Table 1). The recent decline in offshore total phosphorus concentrations, and likely nearshore concentrations, is attributable to the filtering activities of introduced mussels, *Dreissena polymorpha* and *Dreissena bugensis*, in the late 1980s and 1990s. Tributary and other nutrient loads to the nearshore region of the lower lakes are being removed by the filtering activities of abundant, nearshore populations of mussels. In these nearshore areas, mussels are an important sink for phosphorus (Johengen *et al.* 1995), and may even control phosphorus cycling and dynamics (Fahnenstiel *et al.* 1995, Heath *et al.* 1995, Johengen *et al.* 1995). Similar results were noted in Saginaw Bay, where water column phosphorus concentrations decreased by approximately 40% after the introduction of zebra mussels even though phosphorus loadings to the bay were relatively similar throughout the period (Fahnenstiel *et al.* 1995). Thus, the water chemistry of the lower lakes is becoming similar to that of upper lakes due to the dominant input of relatively oligotrophic water from upper Great Lakes via the Detroit River (Chapra and Sonzogni 1979) and the removal of nutrients and other particulates from tributaries and the nearshore region by the filtering activities of non-indigenous mussels.

The similarity in the structure of the microorganism communities of all the Great Lakes in 1993 to 1995, particularly in the spring, is due to the strong influence of abiotic factors. The lack of variability in the biological structure is caused by the similarity of physical/chemical forcing factors. Many of the physical/chemical forcings in these lakes are similar due to their overall similarities in size, morphometry, and geographic position. Recent changes in total phosphorus concentrations in the lower lakes have produced similar concentrations of this limiting nutrient and similar optical characteristics among all the lakes (Table 1); this, in turn, further accentuated the role of physical/chemical factors in controlling the structure of microorganism communities. All of the samples were taken from the offshore waters of the Great Lakes, where regional influences (e.g., riverine inputs, etc.) are minimized due to dilution and large-scale circulation. The large-scale circulation, together with the connecting channels, ensure similarities among the lakes, particularly the influence of the upper lakes on the lower lakes through the transport and mixing of their waters. The importance of physical/chemical factors even extends to stratified conditions when biological control of food-web structure is more likely (Kitchell *et al.* 1988); greater variability in the structure of microorganism communities was noted during stratification (Figs. 4b, 6b), but the overall similarity in structure among stations was still maintained for most groups. It should also be noted that the variability of abiotic controlling factors (e.g., temperature, mean irradiance in mixed layer, mixed-layer depth, total phosphorus concentrations, etc.) also exhibited greater variability in the summer as compared to the spring, so increased variability in food-web structure among stations cannot be attributed easily to biotic factors. Therefore, given the similarities in size and chemistry, their sharing of water through the connecting channels, and the impact of large-scale circulation and mixing, strong similarities in the structure of the planktonic food-web of the Great Lakes should be expected.

The strong similarity in structure of microoorganism communities across the Great Lakes does not preclude the possibility of biological control, but strong biological control would be expected to produce greater variability among the lakes consistent with the variation of abundance and the impact of important organisms (zebra mussels, and vertebrate and invertebrate planktivores) in the different lakes (Holland *et al.* 1995, Nalepa and Fahnenstiel 1995, Rand *et al.* 1995, Yurista and Schulz 1995). Biological control acting primarily through predation can be important in controlling the abundance and structure of microorganism communities; however, in this study evidence of strong biological control of the broad-scale structure of microorganism com-

munities in the Great Lakes was not apparent. It must be emphasized that biological regulation of species abundances within broad taxonomic groups was not part of this investigation. Rather evidence of strong biological control of measured parameters was sought.

One species that has altered many parts of the Great Lakes is the zebra mussel (*Dreissena polymorpha*). Zebra mussels are an important non-indigenous species that have been demonstrated to influence plankton abundance and possibly even phytoplankton species composition in parts of the Great Lakes (Fahnenstiel *et al.* 1995, Holland *et al.* 1995, Lavrentyev *et al.* 1995). In systems impacted by zebra mussels, large changes in particle and plankton abundance, with concurrent changes in optical characteristics and nutrient concentrations, have been noted (Holland *et al.* 1995, Nalepa and Fahnenstiel 1995). Their perceived impact on the broad structure of the microorganism community seems obvious. Yet, the similarity in microorganism structure between Lake Erie, a zebra mussel-impacted lake, and the upper Great Lakes, particularly Lakes Huron and Superior (non-impacted systems), may suggest that zebra mussels are not the dominant direct factor affecting broad-scale structure of the microorganism community. Zebra mussels are contributing to the similarity in microorganism food-web among the lakes by changing bulk or community characteristics (e.g,, optical, nutrient, particle characteristics) of the lower lakes making them more similar to those of the upper lakes, but not necessarily by directly changing grazing differentials among the groups analyzed in this investigation. Because zebra mussels are capable of filtering all major groups of microorganisms (Lavrentyev *et al.* 1995, Horgan and Mills 1997), their lack of a pronounced direct impact on the broad structural groups may not be so surprising. Thus, over short time periods zebra mussel influence is primarily related to regulation of bulk (community) concentrations and characteristics due to the significant increase in overall grazing loss rates among all microorganisms. Over longer time periods, zebra mussels likely directly affect the structural composition of the microorganism community and even species composition within broad taxonomic groups when population-specific grazing differentials are manifested. Quagga mussels (*Dreissena bugensis*) are another important organism with the potential to alter plankton community structure (Dermott and Munawar 1993); at this time, however, there appears to be no evidence of their large-scale impact on the variables measured in this study.

The most-studied aspect of biological control of the food-web structure is associated with vertebrate planktivory, often referred to as top-down control (McQueen *et al.* 1986, McQueen *et al.* 1989). Planktivorous fish can strongly influence the size-structure and species composition of zooplankton communities which, in turn, can influence phytoplankton (microorganism) abundance and composition. The critical link for this top-down control is presence of a keystone species, such as the large-bodied *Daphnia*, *D. pulicaria* or *D. pulex* (Polis and Strong 1996). These top-down effects are primarily manifested during summer stratification (Kitchell *et al.* 1988). Previous work in the Great Lakes has demonstrated strong top-down control of phytoplankton abundance and possibly, even structure in Lake Michigan during the summers of 1983 to 1984 when *Daphnia pulicaria* dominated the zooplankton community due to the collapse of the alewife population (dominant planktivore) (Scavia *et al.* 1986, Fahrenstiel and Scavia 1987). Recent reanalysis of plankton and alewife data from Lake Michigan for the 1954 to 1987 period suggests the linkage between alewife abundance, zooplankton abundance and composition, and phytoplankton abundance was weak and limited to the offshore region of the lake during the summer of 1983 (Evans 1990, 1992). The presence of abundant populations of *Daphnia pulicaria* was critical for the manifestation of top-down control of phytoplankton abundance. Similarly, in Lake Ontario, the crustacean zooplankton community was dominated by small cladocerans and copepods from 1981 to 1991 (Johannsson *et al.* 1991, O'Gorman *et al.* 1997) and no evidence of top-down control of phytoplankton abundance or composition has been reported. Because autotrophic and heterotrophic microorganisms are of similar size, the impact of top-down control would likely extend to all microorganisms, not just phytoplankton.

Given the presence of abundant invertebrate and vertebrate planktivore communities and the dominance of copepods, and/or small-to-medium-sized cladocerans in all the Great Lakes at this time, it is unlikely that planktivory would be important in controlling the broad-scale structure of the microorganism community. In 1993 to 1995, the crustacean zooplankton community of the Great Lakes was dominated by copepods in the spring (> 95% biomass at all stations) and by copepods and/or small-to-medium-sized cladocerans in the

summer. The mean size of the daphnid community was 1.3 mm in Lakes Huron, Michigan, and the eastern basin of Lake Erie, and 0.9 mm in Lake Ontario and the western basin of Lake Erie. Cladocerans were rare in Lake Superior, being found in only one sample where they constituted < 2% of total crustacean biomass. The important large-bodied daphnid, *D. pulicaria*, was found in only two samples from the entire study, where they constituted < 1% of total crustacean biomass.

The lack of strong top-down effects on microorganism community structure in the Great Lakes is likely to continue into the future with a few unplanned exceptions due to present fishery management practices. Given the collapse of the salmon fishery in Lake Michigan in the 1980s resulting from the dramatic declines in alewife abundance, present fish management practice is to maintain a diverse, stable planktivore population in order to sustain the heavily stocked piscivore fishery (Eshenroder *et al.* 1995). This practice has been implemented twice in the 1990s. Concern for declining stocks of planktivores in Lake Ontario (alewife) and the eastern basin of Lake Erie (smelt) resulted in cuts of salmonid stocking rates in these lakes (R. Eshenroder, Great Lakes Fishery Commission, pers. comm). The continued application of this practice in the Great Lakes is expected to produce smaller and fewer declines of planktivore biomass.

Importance of Microbial Food-Web

The functional group (autotrophic:heterotrophic; producers, decomposers, grazers) analysis revealed an abundant microheterotrophic community. Almost all of the heterotrophic microorganism biomass (ca. < 280 μm) was associated with the microbial food-web (protozoans and bacteria), as rotifer and veliger biomass were minor components. Previous work in the Great Lakes, particularly Lakes Michigan and Huron, has demonstrated an abundant and very active microbial food-web (e.g., Scavia *et al.* 1986, Pick and Caron 1987, Taylor and Heynen 1987, Carrick *et al.* 1991, Carrick *et al.* 1992). This work confirms those observations and extends them to all the Great Lakes. Heterotrophic bacteria dominated heterotroph microorganism biomass, contributing 65% of the total and 31% and 22%, respectively, of total microorganism and total plankton biomass. Previous studies in the Great Lakes (Scavia *et al.* 1986, Pick and Caron 1987) and other freshwater environments (Weisse *et al.* 1990, Lyche *et al.* 1996) have found similarly high bacterial biomass. It should be noted that in the highly retentive and autochthonously-driven Sargasso Sea, the ratio of heterotrophic microorganism biomass to phytoplankton biomass was 4 (Fuhrman *et al.* 1989); this value is much higher than the 0.8 ratio found in this study for the Great Lakes.

The large bacterial biomass in all the lakes and the similarity in water chemistry may suggest a stabilizing role for the organic carbon or detrital pool. In small lakes, the dissolved organic carbon (DOC) pool plays an important role as a metabolic regulator and ecosystem stabilizer (Wetzel 1995). This idea was developed for small, allochthonously-driven lakes, but it may have application to the Great Lakes as well. The source of carbon, whether autochthonous or allochthonous, is probably not as important as the pool size and turnover rates of the DOC. Recent changes in concentrations of nutrients in the lower lakes caused by the zebra mussel (Holland *et al.* 1995) likely extend to DOC (Johengen *et al.* 1995). Thus, DOC concentrations may be becoming similar in the lakes and the DOC pool would likely have a unifying role for the heterotrophic communities in the Great Lakes. The role that DOC concentrations play in mediating the structure of the microorganism community in large lakes deserves more attention.

This study documents the important and ubiquitous role that picoplankton-sized organisms occupy in the Great Lakes. Picoplankton biomass (autotrophs and heterotrophs) was approximately equal to the combined biomass of nanno- and microplankton and represented 29% of total planktonic biomass. Previous analysis of nano- and microplankton size organisms using fluorescent microscopy also has documented the importance of picoplankton in the Great Lakes (Fahnenstiel *et al.* 1986, Scavia *et al.* 1986, Pick and Caron 1987, Fahnenstiel and Carrick 1992). This work extends these observations to all the Great Lakes and places them in context with the entire planktonic community. However, not all studies on plankton community structure in the Great Lakes have found abundant and important populations of picoplankton-sized organisms. Sprules *et al.* (1991) and Sprules and Goyke (1994) presented information on the complete biomass size-spectrum for the planktonic communities from Lakes Michigan and Ontario. The unnormalized biomass spectra from both lakes exhibited two distinct peaks for phytoplankton and zooplankton (Fig. 2 in Sprules and Goyke 1994). Their peak in autotroph biomass occurred near 10

μm, and a conspicuous lack of significant biomass in the picoplankton-size fraction (autotrophic and heterotrophic) was found. This lack of picoplankton biomass, at least for their Lake Michigan work, can be related to the use of inappropriate techniques for enumerating picoplankton-sized organisms (Pick and Caron 1987). For the Lake Michigan samples, the Ütermohl technique (Munawar *et al.* 1974) was used to enumerate all autotrophic organisms, from picoplankton to net plankton. The Ütermohl technique, based on inverted microscopy of settled samples, cannot provide accurate estimates of picoplankton-sized organisms (Pick and Caron 1987). The lack of picoplankton biomass reported for the Lake Ontario samples is more difficult to explain, but the results of Sprules and Goyke (1994) are not consistent with the results of this study or with those of Pick and Caron (1987).

When picoplankton biomass is combined with previous growth and production information on planktonic communities in the Great Lakes, it is clear that picoplankton play an important, if not dominant, role in overall community metabolism in the pelagic region of the Great Lakes. Picoplankton-sized organisms exhibit some of the highest growth rates of both heterotrophic and autotrophic organisms in the Great Lakes. For example, in the upper Great Lakes autotrophic picoplankton have a mean growth rate of approximately 0.5/d with a range of 0.1 to 1.5/d (Fahnenstiel *et al.* 1986; Fahnenstiel *et al.* 1991a, b). Nanno- and net phytoplankton exhibit mean growth rates of 0.1/d with a range of 0.1 to 0.5/d (Dorazio *et al.* 1987, Scavia *et al.* 1988, G. Fahnenstiel, unpubl. data). Similarly, in Lake Michigan, heterotrophic protozoans exhibited a mean growth rate of 0.3/d (Carrick *et al.* 1992), whereas heterotrophic bacteria had mean growth rates > 2.0/d (Scavia *et al.* 1986). Previous work on autotrophic and heterotrophic picoplankton productivity has also confirmed the important role that picoplankton sized organisms play in the metabolism of the Great Lakes. Autotrophic picoplankton contribute on average 20% of the total primary productivity in the upper Great Lakes; during summer stratification their contribution can exceed 40% (Fahnenstiel *et al.* 1986, Fahnenstiel and Carrick 1992). Moreover, heterotrophic picoplankton (bacteria) production often exceeds total primary production during the summer in Lake Michigan (Scavia *et al.* 1986, Scavia and Laird 1987). High microheterotroph productivity is possible in highly retentive systems like the Great Lakes because of the recycling potential of organic carbon (Scavia 1988).

Finally, the conclusions of this study were simply a result of new observations of the planktonic food-web; no novel or insightful experiments were conducted. This was a simple, but unique, look at the food-web of the Great Lakes which used the same techniques on the same water samples (at least for microorganisms) from all the lakes. More insights into understanding the food-webs of the Great Lakes will occur when consistent and holistic approachs to sampling, analysis, and interpretation are taken. Some of the difficulty in trying to understand the ecology of the Great Lakes is due to variability in data from studies of limited scope and which employ different sampling methodologies. While this approach is suitable for understanding the factors controlling individual processes or the abundance of specific organisms, it often produces an ecosystem view that is more variable and confusing than all its individual components combined. Given the funding constraints on Great Lakes research in the 1990s, it will be important to apply more holistic approaches to the study of the Great Lakes.

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